

STUDIES ON EUPHAUSIACEAN CRUSTACEANS FROM  
THE INDIAN RIVER REGION OF FLORIDA.  
I. SYSTEMATICS OF THE *STYLOCHEIRON*  
*LONGICORNE* SPECIES-GROUP, WITH EMPHASIS  
ON REPRODUCTIVE MORPHOLOGY

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*Abstract.*—Reproductive organ morphologies in members of the *Stylocheiron longicorne* species-group are compared. Although reproductive structures of 3 of the 7 species are unique, those of *S. microphthalma*, *S. suhmii*, *S. affine*, and *S. longicorne* are very similar, with minor differences possibly attributable to maturity of the structures. Other allegedly species-specific characters (primarily eye structure) are variable and apparently related to size of the individual and habitat depth. The 4 species, interpreted as ontogenetic or ecotypic forms of a single polymorphic species, are synonymized under the name *Stylocheiron suhmii* G. O. Sars, 1883. The reliability of reproductive structures is restored for species diagnoses within the *S. longicorne* species-group to a level consistent with that in other euphausiids.

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Introduction

The morphology of reproductive organs has long been considered important in crustacean taxonomy. When male and female members of a phenon possess unique sexual apparatuses, this suggests that successful interbreeding with other phenon is prevented, promoting the reproductive isolation essential to the biological species concept (Mayr 1969). Similarly, when 2 such phenon differ in certain somatic aspects, yet are identical in sexual morphology, they are usually assumed to belong to a single species because morphological compatibility of reproductive structures implies reproductive compatibility. The observed differences in the 2 phenon must then be explained in other terms, such as individual variation, ecotypic response, or developmental stages.

In euphausiid crustaceans, details of mating and spermatophore transfer are still largely unknown, but the male petasma and female thelycum are generally accepted as being unique within a species. However, according to Brinton (1975), the genus *Stylocheiron* is an exception in that copulatory structures are only of secondary importance in species identification, and body proportions and the structure of the bilobed eye are allegedly more

reliable. Brinton therefore proposed that the mechanisms involved in reproductively isolating the species of *Stylocheiron* must be fundamentally different than those in other euphausiid genera.

The 11 recognized species of *Stylocheiron* have been arranged by Hansen (1910) and subsequent authors into 3 species groups based on the terminal structure of the elongate third thoracic leg. The first group, containing only *S. carinatum* G. O. Sars, 1883, has long, parallel bristles on the propodus and dactyl. Members of the *S. maximum* species group (*S. abbreviatum* G. O. Sars, 1883, *S. maximum* Hansen, 1908, and *S. robustum* Brinton, 1962b) all possess a "true chela" with one major and several minor spines on the propodus, opposing an enlarged, secondarily-spined dactyl. Finally, the *S. longicorne* species group, characterized by a "false chela" formed by opposing sets of curved, serrate spines, consists of 7 species: *S. suhmii* G. O. Sars, 1883, *S. longicorne* G. O. Sars, 1883, *S. elongatum* G. O. Sars, 1883, *S. insulare* Hansen, 1910, *S. microphthalma* Hansen, 1910, *S. affine* Hansen, 1910, and *S. indicus* Silas and Mathew, 1967. Using eye structure, Lomakina (1978) further subdivided this group into the *S. affine* species group, having small pyriform eyes (*S. affine*, *S. suhmii*, *S. microphthalma*, and *S. insulare*), and the revised *S. longicorne* group with larger, more oblong eyes (*S. longicorne*, *S. elongatum*, and *S. indicus*). This arrangement, however, provides no taxonomic advantage over Hansen's *S. longicorne* species group and is therefore unnecessary.

During a survey of the euphausiids of central eastern Florida, 6 species of *Stylocheiron* were encountered. Males of *S. carinatum*, *S. elongatum*, and *S. abbreviatum* all showed sufficiently distinct petasmata for validation of species identifications based on somatic characters. However, the remaining 3 species (*S. suhmii*, *S. longicorne*, and *S. affine*) had nearly identical reproductive structures, but were separable using eye characteristics and body proportions. Thus, whereas the latter 3 species appeared to support Brinton's (1975) statement of unreliability of copulatory structures in *Stylocheiron*, the rule did not apply to others in the genus. The 3 species with similar sexual morphologies all belong to the *S. longicorne* species group. A re-evaluation of the 7 species in the group was therefore undertaken to determine (1) which species show unique, taxonomically reliable, reproductive morphologies, and (2) the degree of variability of other, allegedly more reliable, characters in those species showing similar reproductive morphologies.

### Materials and Methods

Specimens from the central eastern Florida coast were collected by R/V *Gosnold* using a 6-foot Isaacs-Kidd Midwater Trawl at various depths and locations between Sebastian Inlet and Jupiter Inlet (Table 1). Repre-

Table 1.—Data for R/V *Gosnold* stations at which specimens of the *Stylocheiron longicorne* species group were collected.

Sta. no.	Date (1974)	Location	Gear depth (m)	PDR <sup>1</sup> depth (m)	Time (hr, EST <sup>2</sup> )
G-130	17 Jan.	27°02.5'N, 79°58.1'W to 27°09.2'N, 79°58.5'W	50	90	2230–2330
G-131	18 Jan.	27°12.4'N, 79°58.1'W to 27°18.0'N, 79°59.7'W	50	91	0019–0120
G-144	22 Jan.	27°23.3'N, 79°33.5'W to 27°23.4'N, 79°32.7'W	250–75	720	0230–0629
G-159	23–24 Jan.	26°47.1'N, 79°47.3'W to 26°27.6'N, 79°46.7'W	200 <sup>3</sup>	410–393	2030–0006
G-160	24 Jan.	26°49.7'N, 79°46.4'W to 26°50.8'N, 79°47.1'W	300–65	410	0010–0310
G-172	25 Jan.	27°19.7'N, 79°29.9'W to 27°19.8'N, 79°28.5'W	750 <sup>4</sup>	750–700	1530–1807
G-173	25 Jan.	27°20.8'N, 79°28.0'W to 27°20.9'N, 79°27.2'W	150 <sup>3</sup>	700	1827–2100

<sup>1</sup> PDR = Precision Depth Recorder; <sup>2</sup> EST = Eastern Standard Time; <sup>3</sup> estimated depth based on wire out; <sup>4</sup> plankton net hit bottom.

sentative specimens from these collections are cataloged into the Indian River Coastal Zone Museum (IRCZM), Fort Pierce, Florida, the National Museum of Natural History (USNM), Washington, D.C., the British Museum (Natural History) (BMNH), London, the Rijksmuseum van Natuurlijke Historie (RMNH), Leiden, the Instituut voor Taxonomische Zoölogie (Zoölogisch Museum) (ZMA), Amsterdam, the Zoologisk Museum, University of Copenhagen (ZMUC), and the Muséum National d'Histoire Naturelle (MNHN), Paris.

Material examined is listed in the Appendix. Body lengths, whenever cited, were measured (in millimeters) along a dorsomedial line from the tip of the rostrum to the tip of the telson. Specimens were preserved in 70% ethanol. Light microscopy photographs were made using a Wild M-400 Photomakroskop.

Both intact female anterior body portions (for thelycal examinations) and isolated eyes were prepared for scanning electron microscopy using the following procedure. Dehydration at 10 minute intervals in 85%, 95%, and 100% ethanol was followed by 3 solutions of increasing proportions (33.3%, 50%, and 66.6%) of acetone in 100% ethanol, then two 10 minute intervals in 100% acetone. After critical-point drying, the specimens were mounted on standard aluminum stubs with polyvinyl acetate (Bakelite) glue, sputter-coated with gold-palladium for 2 minutes, and examined using a Zeiss Novascan 30 scanning electron microscope.



For examinations using light microscopy, the entire sternal area, including the thoracic legs, was dissected from female specimens for thelycal examinations. Male petasmata were studied on intact first abdominal pleopods. Thelyca and petasmata of the various species were then cleared (from 10 to 15 minutes depending on the size of the specimen) in full-strength household bleach (Chlorox) until all internal tissue had completely dissolved. Partial dissolution of the exoskeleton never occurred, and even the finest setae were left undamaged. When handled carefully to prevent collapsing, high-power examination of the transparent structures (in water or alcohol on a concave slide) afforded an unobstructed view of all processes and setae without further manipulation. This technique allowed the features of the otherwise opaque thelycum to be clearly distinguished, and also eliminated the often-damaging necessity of "unrolling" the petasma to view the arrangement of processes. Line drawings were made from this material using a dissecting stereomicroscope equipped with a camera lucida.

The terms petasma, thelycum, and chela used throughout this paper are consistent with current usage in euphausiid literature, and do not necessarily indicate homology with structures of the same names in decapod crustaceans.

#### Reproductive Structures within the *Stylocheiron longicorne* Species Group

*Petasmata*.—The petasma (Fig. 1A) in the genus *Stylocheiron* is distinguished from that of other genera by the following features. The inner lobe (IL) is fused to the medial lobe (ML) and bears the usual spinous (s), terminal (t), and proximal (p) processes, the latter 2 subequal in size. A minute spine, herein called the secondary spinous process (ss), may be present proximal to the spinous process on the base of the inner lobe. The lateral process (lat) is inserted near the fusion of the inner and medial lobes. The medial lobe is rounded distally and never bears an additional process.

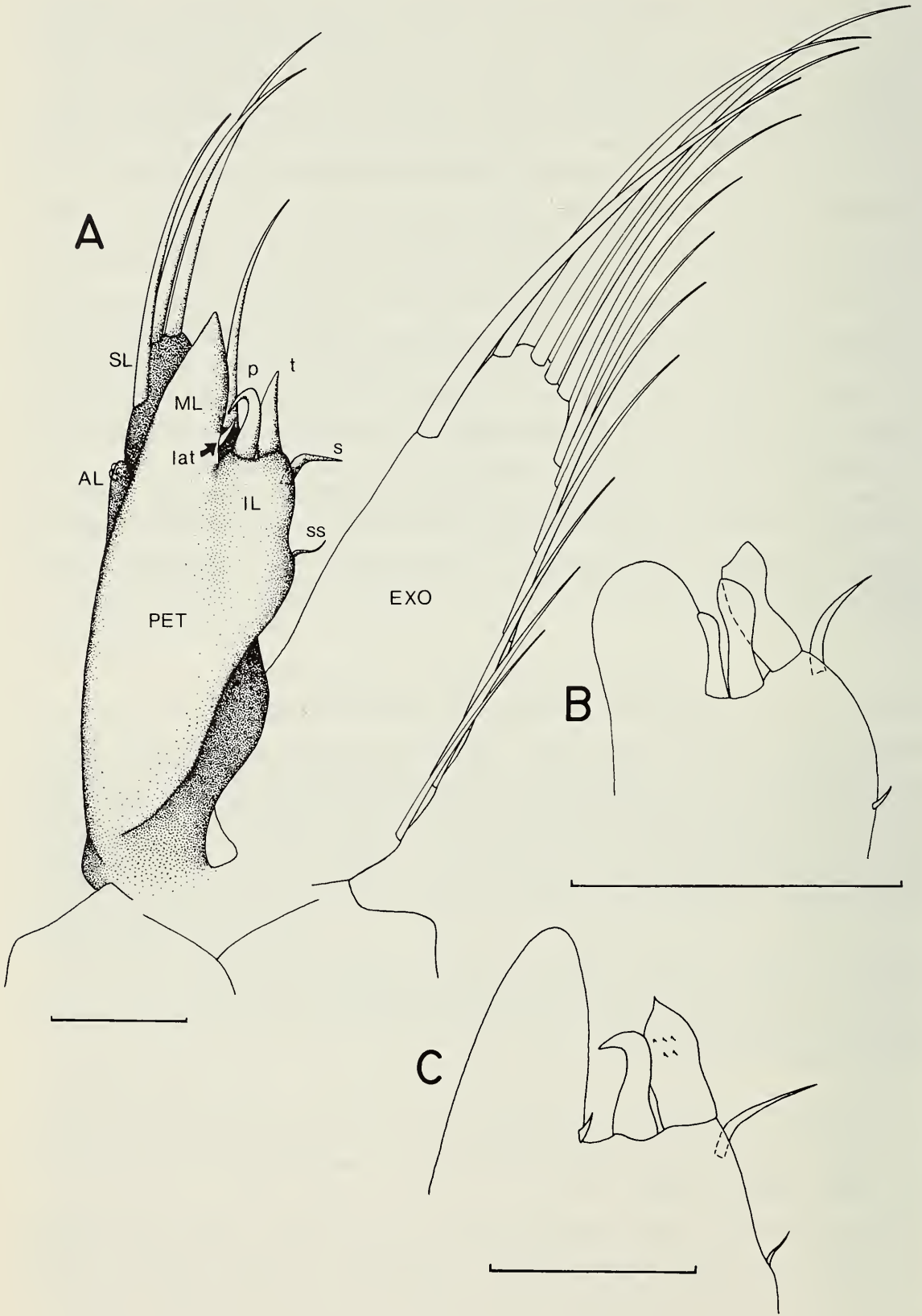
Of the 7 members of the *S. longicorne* species group, 3 species exhibit distinct petasmal features:

*S. elongatum* (Fig. 1A)—terminal process slender, acutely tapering; proximal process distally tapering and hooked; lateral process acute, minute (i.e., less than half height of terminal or lateral process) (G. O. Sars 1885; Brinton 1975).

*S. insulare* (Fig. 1B)—terminal process wide basally, tapering, obliquely truncate distally; proximal process tapering, rounded distally; lateral process rounded distally, more than half height of terminal or lateral process (Hansen 1910; Brinton 1975).

*S. indicus* (Fig. 1C)—terminal process broad, distally acute, curving posteriorly over concavity bearing 5–6 tooth-like processes in 2 rows; prox-





imal process distally acute, strongly hooked; lateral process minute (Silas and Mathew 1967; Brinton 1975).

The remaining 4 species in the group show nearly identical petasmas structures, with subequal terminal and proximal processes with rounded distal ends. The lateral process is only slightly smaller than the other processes and is of similar shape. The 4 species are distinguished from one another in the literature by the following characteristics:

- S. microphthalma* (Fig. 2A)—terminal process distally rounded; proximal process subequal to terminal process, distally produced; both processes distally smooth (Hansen 1910).
- S. suhmii* (Fig. 2B)—terminal and proximal processes similar in shape and size, distally smooth (Boden *et al.* 1955).
- S. affine* (Fig. 2C)—terminal and proximal processes similar in size and shape; former armed distally with 2–3 teeth (Hansen 1910).
- S. longicorne* (Fig. 2D)—similar to *S. affine*, except terminal process with 6 teeth (Hansen 1910).

Such differences noted by previous workers are not sufficient to warrant specific separation. Material examined from all 4 “species” indicated that these differences, as well as oft-cited proportions of the processes, are well within the limits of individual variation, as seen, for example, in the range of variability documented by Banner (1950) in the petasmata of *S. maximum*. Moreover, differences noted in the proximal processes may be a result of viewing angle rather than the actual shape of the process itself. Petasmata are conventionally examined by “unfolding” the structure prior to examination. This manipulation results in a variety of viewing angles depending on the degree to which the petasma has been flattened. Thus, the bladelike proximal process may appear either broadly rounded or slightly produced according to orientation of the petasma.

The serrations of the terminal process in *S. affine* and *S. longicorne* are also not taxonomically significant. These 2 species respectively attain the second largest and largest adult sizes of the 4 under consideration (see below). Therefore, serrations may either appear only on petasmata of larger

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Fig. 1. Petasmas structure in the *Stylocheiron longicorne* species group: A, *S. elongatum*, 9.1 mm male, Gosnold Sta. 144; posterior view of entire first left pleopod; B, *S. insulare*, 6.5 mm male (adapted from Hansen 1910, and Brinton 1975); median and inner petasmas lobes; C, *S. indicus*, 8.75–12.0 mm male (adapted from Silas and Mathew 1967; length not specific); median and inner petasmas lobes. AL, auxiliary lobe; EXO, exopod; IL, inner lobe; ML, median lobe; PET, petasma; SL, setiferous lobe; lat, lateral process; p, proximal process; s, spinous process; ss, secondary spinous process; t, terminal process. Scale = 1.0 mm.

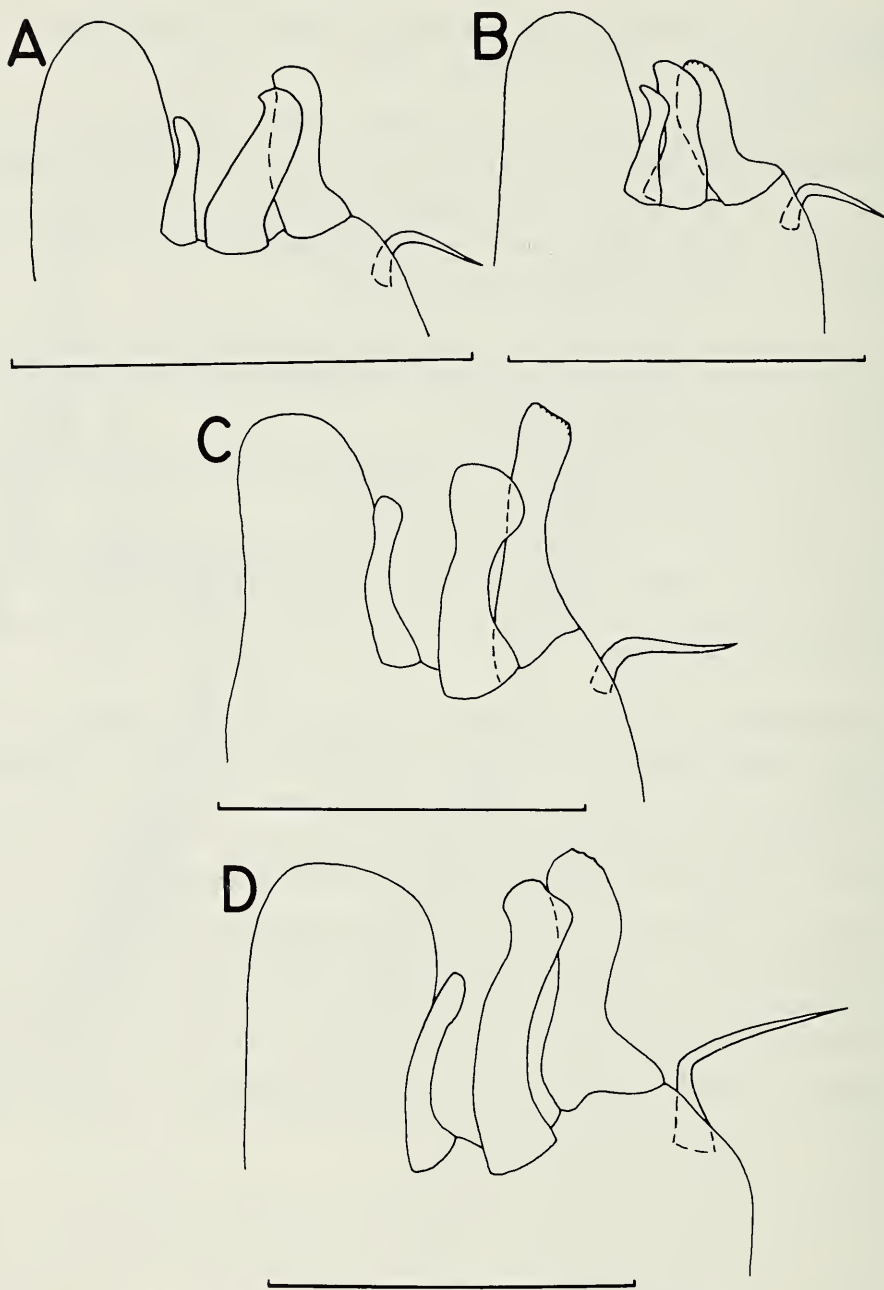


Fig. 2. Posterior views of median and inner petasmas in the *Stylocheiron longicorne* species group. Orientation and scale as in Fig. 1. A, *S. microphthalmum*, 5.5 mm male (adapted from Hansen 1910, and Boden *et al.* 1955); B, *S. suhmii*, 5.9 mm male, Gosnold Sta. 160; C, *S. affine*, 6.5 mm male, Gosnold Sta. 144; D, *S. longicorne*, 9.1 mm male, Gosnold Sta. 144.

individuals, or may merely be an indication of the full maturation of the structure. The latter contention is supported by my observation of a distally serrate terminal process on the petasma of a 5.9 mm male of *S. suhmii* (Fig. 2B), a form in which the terminal process is allegedly smooth.

*Thelyca*.—The diagnostic value of the female thelycum in euphausiids is



generally accepted (Einarsson 1942; Costanzo and Guglielmo 1976a), but the structure has not been examined in all species. In the *S. longicorne* species group, only the thelyca of *S. suhmii* and *S. longicorne* have been described (Costanzo and Guglielmo 1976b). In the present study, thelycal structures from eastern Florida specimens of *S. elongatum*, *S. suhmii*, *S. affine*, and *S. longicorne* were examined; material of *S. microphthalma*, *S. indicus*, and *S. insulare* was insufficient for dissection and study.

As in other species of *Stylocheiron* (see Costanzo and Guglielmo 1976b), the thelycum of *S. elongatum* (Fig. 3A) is formed solely by the plates from the coxae of the sixth thoracic legs. The plates join mid-ventrally in the anterior half of the thelycum, forming a prominent ridge. Posterior to the ridge, the medial edges of the plates are free and parallel one another, then diverge at 180° before joining the posterior edges of the plates. A pair of stalked, oblong spermatophores (each 0.21 mm long, 0.07 mm wide, with a 0.15 mm long stalk) may be implanted in the quadrate spermatophore pocket (sp) formed by the plates. Four long, sparsely plumose setae, herein called primary setae (s'), originate from a flap on each side of the anterior portion of the thelycum, lateral to the mid-ventral ridge. Dorsal to this row lie 2 stout, plumose setae, herein called secondary setae (s'').

Costanzo and Guglielmo (1976b) reported a similar configuration for the thelyca of *S. suhmii* and *S. longicorne*. These 2 species differ from *S. elongatum* in that the plates are fused only in the anterior third of the mid-ventral area, and the free edges diverge immediately posteriorly, forming a V-shaped opening. The spermatophore pocket is shallow and U-shaped, rather than deep and quadrate as in *S. elongatum*, although the single or paired spermatophores are of a shape and size similar to that species. My study confirms the thelycal morphologies of *S. suhmii* and *S. longicorne* reported by Costanzo and Guglielmo (1976b), and shows that a similar configuration exists for *S. affine*. These 3 species appear to differ from one another only in the numbers of primary and secondary setae present at the anterior edge of the thelycum:

*S. suhmii* (Fig. 3B)—3 primary, 2 secondary setae (Costanzo and Guglielmo 1976b); 2–3 primary, 2 secondary setae (present study).

*S. affine*—3–4 primary, 2 secondary setae.

*S. longicorne*—5 primary, 4 secondary setae (Costanzo and Guglielmo 1976b). Specimens in the present study were divided according to eye and abdominal proportions into the “long” and “short” forms of Brinton (1962a) (see below). The “long” form exhibited the 5 primary and 4 secondary setal pattern previously reported; the “short” form showed 3 primary and 3 secondary setae.

The identical morphology, the variable and overlapping setal counts, and the increasing number of setae progressing from *S. suhmii* to *S. affine* to

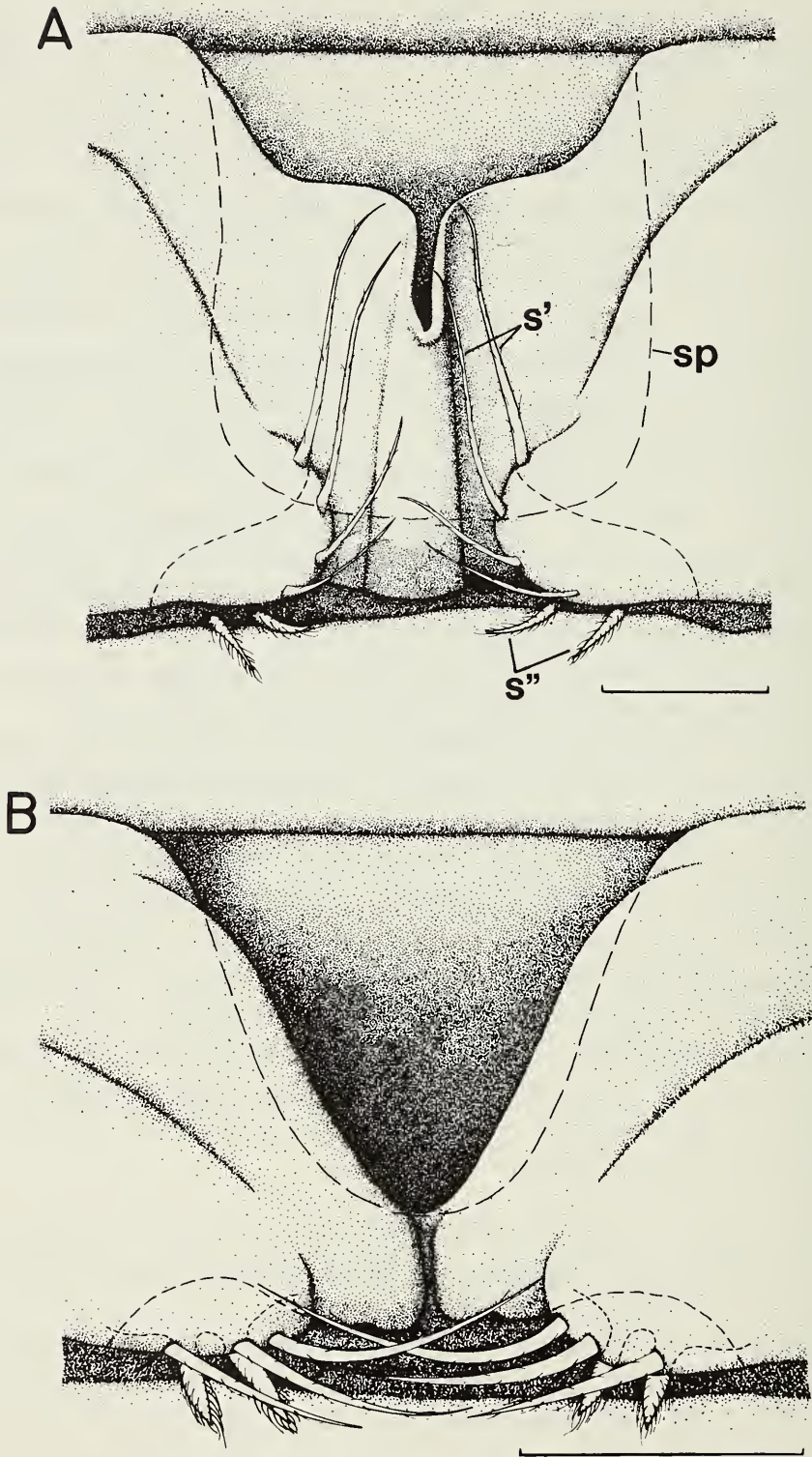


Fig. 3. Thelycal structure in the *Stylocheiron longicorne* species group. Ventral view of sixth sternal segment; posterior edge is at top of plate. A, *S. elongatum*, 13.9 mm female, Gosnold Sta. 144; B, *S. suhmii*, 7.4 mm female, Gosnold Sta. 159. sp, spermatophore pocket; s', primary setae; s'', secondary setae. Scale = 1.0 mm.



*S. longicorne* (thus roughly with increasing body size), indicate that the thelycal structures are not sufficiently unique to be characteristic of 3 different species. Moreover, because of the similarity shown by the petasmata in males of the 4 species, I suspect that the thelycum of *S. microphthalmia* should correspond closely in structure to those of females of the other 3 species.

The male and female reproductive anatomies of these 4 *Stylocheiron* species, as currently defined, are not species-specific in the sense utilized in other euphausiid descriptions. Brinton (1975) stated that copulatory structure in *Stylocheiron* is less reliable than other characters, but this unreliability may be the result of conferring specific status to 4 phena of a single species, because other members of the *S. longicorne* species group (as far as they have been examined) show structures sufficiently distinct to maintain specific ranking. Reduction of these 4 phena to conspecific status can be supported by other data, so that the reliability of reproductive morphology in these taxa can be restored. In the following sections, other reported morphological and ecological differences among the 4 "species" are re-examined in light of the polymorphic species hypothesis (see Table 2).

It is noteworthy that Brinton (1962a, 1975) described 5 forms of *S. affine* and 3 of *S. longicorne* from the Pacific and Indian Oceans, on the basis of greater variability in proportions of the eye and sixth abdominal segment than that shown by other members of this species group. However, geographic distributions within Brinton's study area of the forms of each species show slight overlap, suggesting that the observed morphological variation may be at least partly environmentally influenced. In my analysis, however, measurements and meristics of *S. affine* and *S. longicorne* will encompass the values for all forms of these species (*sensu* Brinton) combined under their respective species headings.

### Eye Morphology

The single most important taxonomic character presently used to separate the 4 species is the number of enlarged ommatidia comprising the upper lobe of the eye. Hansen (1910) and subsequent authors counted ommatidia in lateral view using either (1) the aligned rows of bulbous external facets outlined at the upper edge, or (2) the internal crystalline cones within adjacent ommatidia. With this traditional method, only the most lateral ommatidia are seen, so that only a partial count is provided. Currently accepted ommatidial meristics for the 4 species increase progressively from *S. microphthalmia* through *S. longicorne* (Table 2).

The partial ommatidial count using the lateral view of the eye has been consistently used as a taxonomic character, so total number of ommatidia has been infrequently recorded. Hypothetical geometric arrangements of



Table 2.—Comparative adult characteristics of *Stylocheiron microphthalmum*, *S. suhmii*, *S. affine*, and *S. longicorne*.

	<i>S. microphthalmum</i>	<i>S. suhmii</i>	<i>S. affine</i>	<i>S. longicorne</i>
Number of specimens examined <sup>1</sup>	23	215	74	76
Eye:				
Number of rows of facets visible in lateral view	2 <sup>a</sup>	3 <sup>a</sup>	4–8 <sup>e</sup>	7–19 <sup>e</sup>
Total number of facets (hypothetical)—see Fig. 4)	4	7	14–52	30–271
Eye length (mm)	0.40–0.58 0.49–0.54 <sup>e</sup>	0.55–0.75 0.57–0.61 <sup>e</sup>	0.70–1.20 0.61–1.25 <sup>e</sup>	0.70–1.48 0.81–1.46 <sup>e</sup>
Eye length	1.45–2.11	1.53–2.14	1.63–2.33	1.93–3.25
Width of lower lobe	±2.0 <sup>a</sup>	2.0 <sup>b</sup>	1.5–2.0 <sup>h</sup>	2.0 <sup>a</sup>
Width of lower lobe	2.25–3.67	1.85–3.25	1.27–2.18	0.76–1.21
Width of upper lobe	2.5–3.0 <sup>e</sup>	3.9–4.3 <sup>e</sup>	1.45–2.55 <sup>e</sup>	0.86–1.44 <sup>e</sup>
Ommatidial diameter (μ):				
Upper lobe	42	50	56 [6] <sup>2</sup>	52 [7]; 60 [13]
Lower lobe	12	20	23 [6]	27 [7]; 32 [13]
Adult size:				
Average cited body length (mm)	5.5–6.4 <sup>a</sup>	6.0–7.0 <sup>e</sup>	5.8–8.5 <sup>e</sup>	6.5–13.0 <sup>c</sup>
Maximum recorded body length (mm)	7.0 <sup>e</sup>	7.9 <sup>d</sup>	11.1 <sup>d</sup>	15.3 <sup>d</sup>
Eye length <sup>e</sup> Body length	0.079–0.087	0.077–0.105	0.097–0.160	0.108–0.149
Length/depth of sixth abdominal segment	1.43–1.89 1.46–1.60 <sup>e</sup>	1.50–1.92 1.66–1.69 <sup>e</sup>	1.16–1.87 1.40–2.55 <sup>e</sup>	1.19–2.15 1.63–2.60 <sup>e</sup>
Length/width of antennal scale	12 <sup>a</sup>	13–14 <sup>b</sup>	13–14 <sup>a</sup>	13–15 <sup>a</sup>
Fecundity <sup>f</sup>	10–13	8–15	4–12	6–16
Thoracic integumental sensilla: <sup>g</sup>				
Length of entire structure (mm)	ND <sup>3</sup>	1.50	1.41	1.23
Length of major group (mm)	ND	0.47	0.47	0.35
Depth distribution: area of maximum abundance (m):				
Discrete depth collections:				
Brinton 1967	ND	0–200	50–250	100–350
Baker 1970	ND	0–100	0–150	50–460
Schroeder 1971	ND	0–400	140–400	200–300
Depth range collections:				
Ponomareva 1963	0–200	0–300	0–500	0–500
Roger 1974a	0–150	0–200	0–400	50–500

Data from: a, Hansen 1910; b, Hansen 1912; c, Boden *et al.* 1955; d, Schroeder 1971; e, Brinton 1975; f, Roger 1976; g, Mauchline and Nemoto 1977 (approximate measurements based on illustration); h, Lomakina 1978.

<sup>1</sup> Original data (without superscripts) are based on examination of Floridan specimens of *S. suhmii*, *S. affine*, and *S. longicorne*, and of the syntypes of *S. microphthalmum* (see Appendix).

<sup>2</sup> Lateral number of rows in the upper eye lobe in the variable *S. affine* and *S. longicorne* as indicated in brackets.

<sup>3</sup> ND = no data.

hexagons, verified by SEM and light microscopy of the actual ommatidia, yielded 2 general patterns (Fig. 4). The first pattern, based on the eye of *S. microphthalmia* with 2 rows in lateral view (Fig. 5A), is seen in all eyes with an even number of rows in lateral view. Initial observation of the eye of *S. microphthalmia* indicated a total of 3 ommatidia (Fig. 5B), but closer scrutiny revealed a fourth, slightly smaller facet. This ommatidium must be included in the total of the upper lobe because it possesses a crystalline cone, a structure lacking in the rudimentary cells of the lateral areas (Kampa 1965). The resultant total of 4 ommatidia for *S. microphthalmia* agrees with that previously reported by Brinton (1967).

The even-numbered ommatidial pattern increases in size by the addition of facets around the perimeter of the 4-faceted core (Fig. 4A). Addition of a single ring of facets produces a hypothetical eye with 4 rows in lateral view and a total of 14 facets. Such an eye is indicative of *S. affine* (which may have from 4 to 8 rows in lateral view) but disagrees with Brinton's (1967) minimum total of 16 for this species.

Caution must be used when viewing eyes exhibiting the even-numbered format. Distortion of the eye may cause an improper anterolateral viewing angle, 60° clockwise from lateral, to be used. A miscount results because this angle yields an "incorrect" number of rows, i.e., one row greater than that generated in direct lateral view. For example, an eye with 6 rows in lateral view (indicated by solid arrows in Fig. 4A) yields an "incorrect" count of 7 rows when viewed from an anterolateral angle (open arrows in Fig. 4A). As will be discussed below, this error led to Hansen's (1910) misinterpretation of eye meristics in the holotype of *S. suhmii*, and the unnecessary establishment of his species *S. microphthalmia*.

The second generalized ommatidial pattern (Fig. 4B), seen in eyes with an odd number of laterally viewed rows, is based on a core of 7 hexagonal facets, exhibited by the eye of *S. suhmii* (Fig. 5D) with 3 rows visible in lateral view (Fig. 5C). This disagrees with the total of 8 ommatidia reported for this species by Brinton (1967). The number of facets increases in the same manner as in the even-numbered pattern, i.e., by the addition of cells around the perimeter. Misinterpretation of the number of rows in this type of eye is not a problem because lateral and anterolateral counts are identical.

Predicted totals for each species, according to currently accepted lateral counts, are listed in Table 2. In *S. longicorne*, the number of rows in lateral view is large, and the facets of the upper lobe are only slightly enlarged relative to those of the lateral areas (Fig. 6E-F). Total number of facets in such an eye is difficult to determine and examination of crystalline cones is necessary to delimit upper from lateral areas. This count is presently of little practical use, but expected totals are included in Fig. 4 and Table 2 for the sake of completeness.

Brinton's (1975) data on number of eye facets in lateral view compared with adult body length (Table 2) indicate that larger specimens should pos-

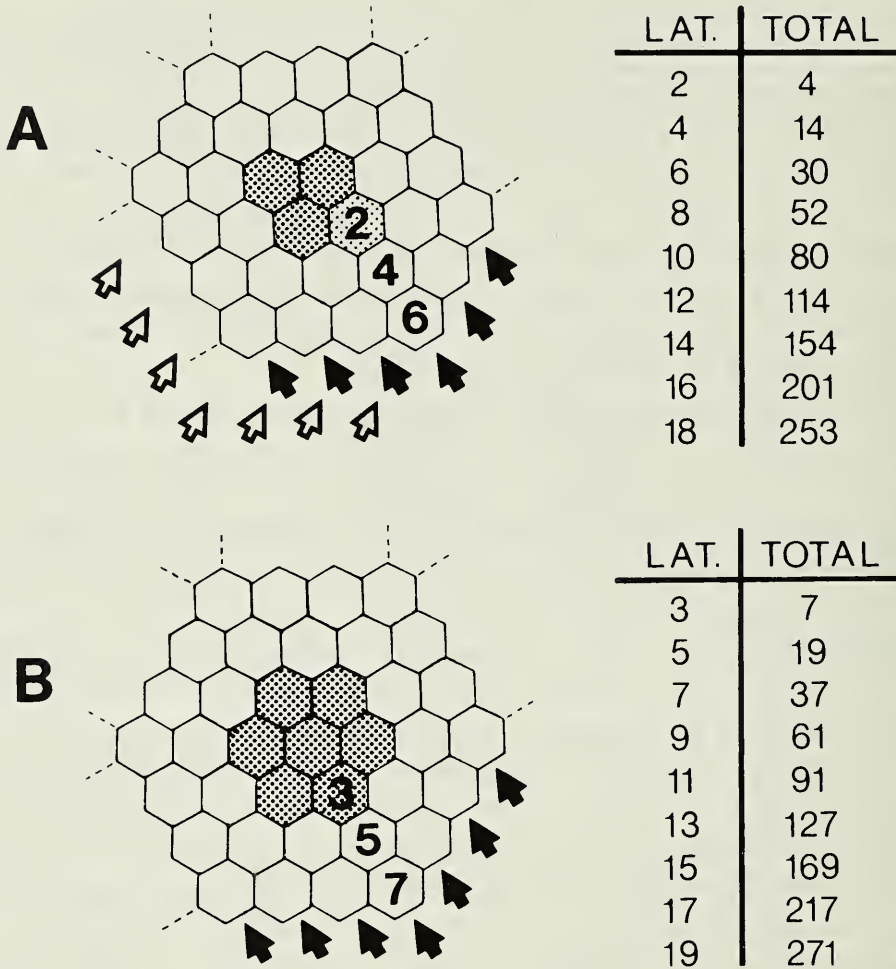


Fig. 4. Schematic ommatidial arrangement in *Stylocheiron*. A, Pattern for eyes with even number of facet rows in lateral view. Core structure is that of *S. microphthalmum* (smaller fourth facet (see text) indicated by lighter stippling). B, Pattern for eyes with odd number of facet rows in lateral view. Core structure is that of *S. suhmii*. Solid arrows indicate angle of lateral view. Open arrows indicate "incorrect" anterolateral viewing angle. Charts list lateral counts and associated expected totals.

sess more facets. However, my examinations of eastern Florida specimens of *S. suhmii*, *S. affine*, and *S. longicorne*, plus the syntypes of *S. microphthalmum* (from the Indo-Pacific), show that for a single given body length, a variety of eye structures may be found. For example, lateral counts of 2, 3, 6, and 7 facets were observed in specimens of identical body lengths. This indicates that eye structure is not strictly a size-related character, as Brinton's data suggested.

Other values pertaining to the eyes are frequently cited for these species (Table 2). (1) Length of the eye, as expected, generally increases with maximum body length (see below). However, data from the present study revealed even greater overlap than that reported by Brinton (1975), indicating that eye length is extremely variable and therefore not taxonomically useful.



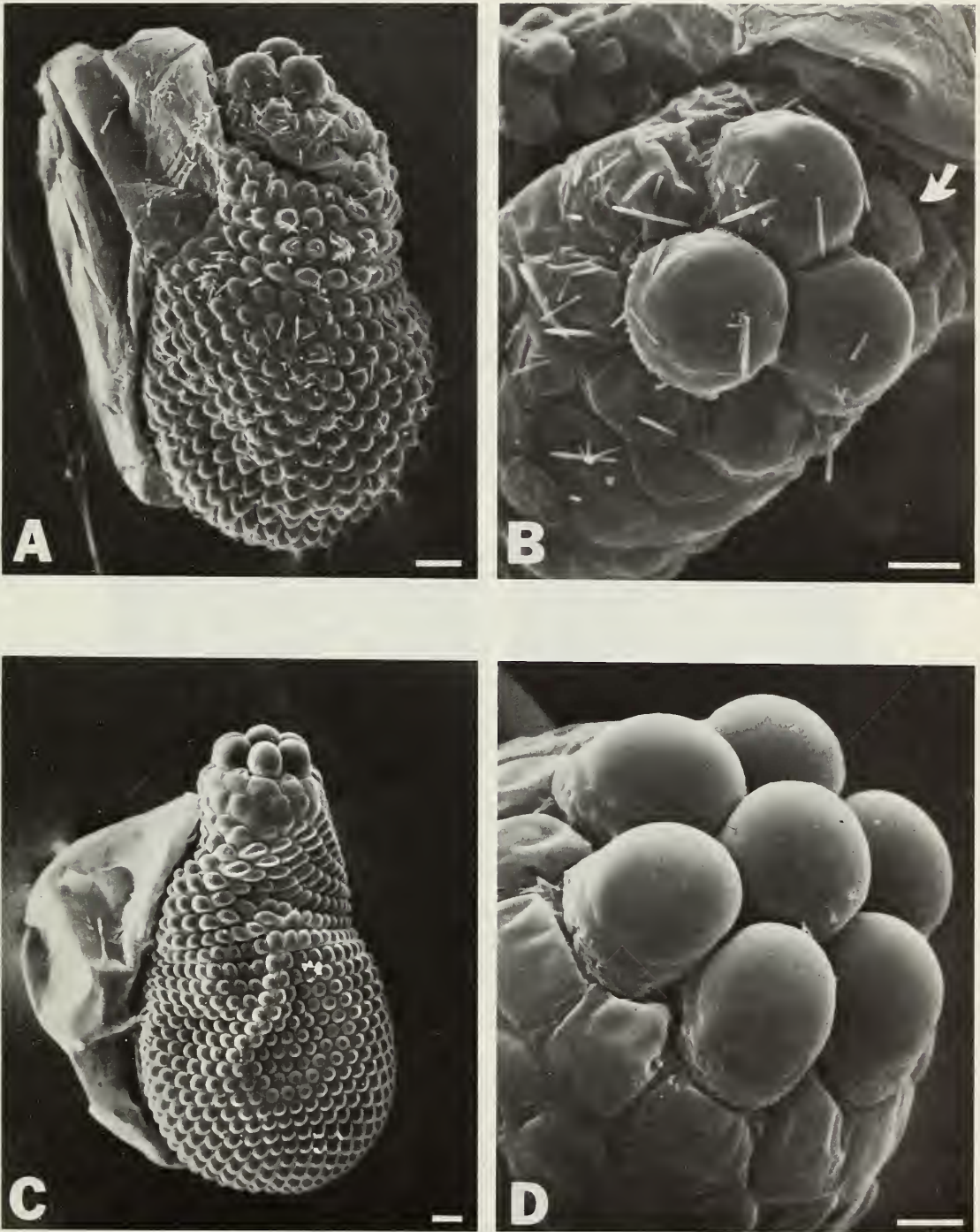
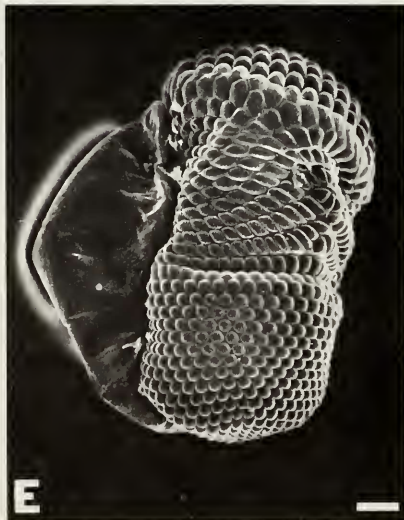


Fig. 5. Scanning electron micrographs of the eyes of *Stylocheiron*: A, *S. microphthalmum*, right eye, male, USNM 49355; B, Same, enlarged view of upper lobe, arrow indicates smaller fourth ommatidium (see text); C, *S. suhmii*, right eye, female, Gosnold Sta. 160; D, Same, enlarged view of upper lobe. Scale = 40  $\mu$  (A, C), 20  $\mu$  (B, D).

(2) The ratio of eye-length to width of the lower lobe, generally recorded as  $\pm 2.0$  for all 4 species, was confirmed by this study. (3) The ratio of the widths of the upper and lower lobes of the eye showed some overlap but in general decreased with increasing number of facets in the eye. Brinton's





(1975) data for *S. suhmii*, however, do not fit the general pattern found by him in the remaining 3 species, and by me in all 4 species. Because the upper eye width depends on the number of facets, a decrease in lobe ratio seems logical. Such a decrease was supported by measurements from SEM preparations (see Figs. 5–6 and Table 2) wherein ommatidial diameter increased in both lobes relative to increasing eye length and number of facet rows. The lobe ratio also illustrates the main feature subjectively used in this study to separate specimens of *S. affine* and *S. longicorne* having identical lateral row counts, namely, the width of the lower lobe. *S. affine* exhibited a distinctly pyriform eye, with a wider lower lobe (Fig. 6A), whereas the eye of *S. longicorne* was oblong with lobes of nearly equal width (Fig. 6C and E). No overlap in this ratio in these 2 species occurred either in Brinton's (1975) data or that of the present study. However, the dependence of this ratio on number of facets in the upper lobe means that the number of facets per se, previously used to separate species, is not a taxonomically valuable character.

#### Adult Size

Average and maximum recorded adult lengths are listed in Table 2. Both values generally increase as one progresses from *S. microphthalmia* through *S. longicorne*. Although this does not rule out the possibility of 4 specimens having equal body length yet morphologically distinct eyes, it does indicate that animals with larger eyes do attain greater body lengths. Regrettably, data indicating the degree of variability in eye morphology within each form during its life history are unavailable.

The ratio of eye-length to body-length reflects an allometric increase in size of the eye relative to the body as overall size increases. As with eye length alone, this character displays considerable variation and overlap between species, and therefore is of limited taxonomic value.

#### Abdominal Morphology

Second in taxonomic value to characteristics of the eye among these 4 species has been the length-to-width ratio of the sixth abdominal segment.

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Fig. 6. Scanning electron micrographs of the eyes of *Stylocheiron*: A, *S. affine*, left eye, female, Gosnold Sta. 144, 6 rows of facets in lateral view; B, Same, enlarged view of upper lobe, total of 30 facets; C, *S. longicorne* ("short form" of Brinton 1962a), left eye, female, Gosnold Sta. 144, 7 facet rows in lateral view; D, Same, enlarged view of upper lobe, total of 37 facets; E, *S. longicorne* ("long form" of Brinton 1962a), right eye, male, Gosnold Sta. 172, 13 facet rows in lateral view; F, Same, enlarged view of upper lobe, left eye, female, Gosnold Sta. 160, approximately 15 facet rows in lateral view. Scale = 100  $\mu$  (A, C, E, F), 40  $\mu$  (B, D).



Brinton's (1975) data from Pacific specimens (see Table 2) showed sufficient overlap to preclude this character being used alone to identify species. Furthermore, Atlantic specimens (see Table 2, original data) revealed even greater overlap, indicating this character to be extremely variable and thus of limited taxonomic value, at least for Atlantic material.

### Other Morphological Characteristics

Other features recorded in the literature, although presumably species-specific, have not been accorded as much taxonomic value as those already discussed (see Table 2). These include:

(1) The length-to-width ratio of the antennal scale, which increases with increasing body length.

(2) Fecundity, in terms of numbers of ova in a mature female ovary (Roger 1976). These data were based on a very small number of specimens examined and showed no conclusive trend.

(3) The arrangement of thoracic integumental sensilla, believed to function as light receptors. This has only recently been reported (Mauchline and Nemoto 1977) in 3 of the species under consideration (that of *S. microphthalmalma* has not been examined). The structure is morphologically similar in all 3 species and consists of 4 small sensilla, quadrangularly arranged, plus a larger oblong sensillum, surrounded by 4 of smaller size. Both the length of the entire arrangement of sensilla and the length of the major sensilla group decrease slightly with increasing body length.

(4) Structure of the maxillae. Of the 7 elements of euphausiid mouthparts (labrum, mandibles, labia, maxillulae, maxillae, first and second thoracic limbs), only the maxillae are consistent enough in structure to be of taxonomic value in the genus *Stylocheiron*. Although the mouthparts of *S. microphthalmalma* have not been examined, the maxillae of *S. suhmii*, *S. affine*, and *S. longicorne* are similar in general configuration (Mauchline 1967). Furthermore, the maxillae in these 3 species lack the suture line, present in all other examined *Stylocheiron* species, that marks the fusing of the lobe of the third joint with the endopod. No other characteristics, such as setal arrangements or types, are useful in distinguishing the maxillae of these 3 species from each other.

(5) Structure of the "false chelae." Observations of the "false chelae" of Floridan *S. suhmii*, *S. affine*, and *S. longicorne* using SEM showed them to be similar in overall structure to previously published accounts for all 4 species under consideration. The propodus bears 3 "serrate" spines of varying length, opposing 5 similar spines on the dactyl. The shortest and most medial of the 3 propodal spines has a distinct 90° bend at its tip in all 4 species under consideration, a feature also evident in *S. insulare* (see Hansen 1910). (In *S. elongatum* (personal observation) and *S. indicus* (see Silas

and Mathew 1967), the spine is only slightly curved.) Although the serrations of these spines appear as small denticles under the light microscope, SEM showed them to be composed of imbricated cuticular plates. Boden *et al.* (1955) stated the serrations to be finer in *S. suhmii* than in *S. affine* or *S. longicorne*; this was the only distinction among the chelae of these species reported in the literature.

### Larval Development

Morphological data from larval studies of all 4 species (Table 3) are both incomplete and unreliable, being based on collected, rather than laboratory-cultured, larvae. Identifications therefore rely on similarity to whatever adult species were collected in the same area, often including more than one of the 4 species in question. However, assuming the larvae belong to the 4 species as a group, the data provided by these studies suggest similar developmental sequences among those "species" in which larvae have been described. Considerable variation is also evident, especially in pleopodal setational sequences in furcilia larvae. Mauchline (1959) suggested that changes in these appendages in euphausiids are a result of environmental influences, resulting in a series of dominant stages plus a number of less-frequently encountered variants. If so, other structures, such as the eye, might also be altered by environment during larval or post-larval development.

### Depth Distribution

All 4 species are generally considered to be epi- to mesopelagic, and non-migratory. Collections made with opening-closing nets to sample discrete depth intervals (Brinton 1967; Baker 1970; Schroeder 1971) revealed populations of *S. suhmii*, *S. affine*, and *S. longicorne* to be centered at overlapping, but respectively deeper, levels (Table 2), thus paralleling the increasing number of facets in the upper eye lobe. Although *S. microphthalma* was not found in these 3 investigations, data from other collections indicate this species occurs, as expected, at generally shallower depths than the other 3 species (Ponomareva 1963; Roger 1974).

### Discussion

These data suggest 2 alternatives. The 4 species are either (1) sibling species (as held traditionally) in which genetically-induced eye morphology determines habitat depth, which in turn acts to isolate allopatrically the various phena, or (2) a single species, the life history of which includes a series of sequentially-varying eye morphologies, which in turn dictate habitat depth. Accordingly, shallow-living small individuals with few eye facets

Table 3.—Comparative larval characteristics of *Stylocheiron microphthalmum*, *S. suhmii*, *S. affine*, and *S. longicorne*.

	<i>S. microphthalmum</i> <sup>1</sup>	<i>S. suhmii</i> <sup>2</sup>	<i>S. affine</i> <sup>3</sup>	<i>S. longicorne</i> <sup>4</sup>
Calyptopsis:				
Body length (mm)	ND <sup>5</sup>	1.2–2.5	ND	1.3–2.4
Number of abdominal segments	ND	0→5→6	ND	ND
Number of terminal telson spines	ND	5→6 or 6	ND	6→7
Eye structure	ND	pyriform	ND	ND
Furcilia:				
Body length (mm)	ND	2.2–3.3	ND	1.9–4.0
Pleopod setation sequence: <sup>6</sup>				
		(0"0')→	(0"0')→	(0"0')→
		(0"1')→	(0"2')→	(0"1')→
Dominant stages	ND	(1"2')→	(1"2')→	(1"2')→
		(3"2')→	(3"2')→	(3"2')→
		(5")	(5")	(5")
Variant stages	ND	(0"2');(2"3'); (4"1');(1"0')	(0"1');(4"1')	ND
Number of terminal telson spines	ND	6→4→1 or 6→4	5→3→1 variant of 3	7→5→1 or 7
Number of facet rows in upper eye lobe	2	2–3 or 2	3	3–5 or cylindrical, and 3–4
"Cyrtopia" (now considered late furcilia stages):				
Body length (mm)	ND	3.0–4.0	ND	3.6–4.9
Number of terminal telson spines	ND	1	ND	7→1 or 5→1
Number of pairs of long lateral telson spines	ND	2→1	ND	2→1

Data from: <sup>1</sup> Brinton 1962a. <sup>2</sup> Brinton 1975; B. Casanova 1972, 1974; Gurney 1942; Lebour 1926 (a–c). <sup>3</sup> Brinton 1975; Silas and Mathew 1977. <sup>4</sup> B. Casanova 1972, 1974; Frost 1935; Mauchline 1971. <sup>5</sup> ND = no data. <sup>6</sup> Pleopod designations: (stage and setation) " = setose; ' = nonsetose.

should develop into larger individuals with larger eyes, capable of inhabiting greater depths. Current taxonomy in these 4 species advocates the first choice. However, morphological, ontogenetic, and ecological information now available, although admittedly incomplete, equally (and in some cases, better) supports the second hypothesis.

*Morphology.*—The similar reproductive morphologies show that *S. microphthalmum*, *S. suhmii*, *S. affine*, and *S. longicorne* possess greater affinities to one another than to other members of the *S. longicorne* species group. Other data indicate that the current taxonomic practice of relying almost exclusively on the upper lobe of the eye for separation of these



species is of questionable value. This upper lobe has been shown to increase in both size and number of ommatidia with increasing habitat depth, probably as a function of light penetration levels. J. P. Casanova (1977) found this same relationship in the spherical-eyed *Meganyctiphanes norvegica*; specimens from Atlantic surface waters had eyes of smaller overall diameter, ommatidial diameter, and number of ommatidia, than deeper-living Mediterranean specimens. The specialized upper lobe in euphausiids with bilobed eyes is known to function in distance perception (Mauchline and Fisher 1969), vital to predatory animals, so that a greater number of ommatidia would presumably be required at the lower light levels occurring at greater depths. Although Brinton (1967, 1975) recognized this relationship as adaptation related to visual recognition of prey, potential mates, and predators, he did not consider the alternative that only one instead of 4 species might be involved.

Other morphological differences between the 4 forms are also compatible with the single-species hypothesis. Observed size differences in thoracic compound sensilla, believed to be involved in light perception, indicate that these structures also contribute to attainment of appropriate light intensity levels and depths. Furthermore, the existence of sexually mature and ovigerous members of all 4 forms of the species is explained if an individual becomes sexually mature at a small size, remains reproductively active as it becomes larger and the number of eye facets concomitantly increases.

*Ontogeny.*—Larvae described in the literature, although questionably labelled with 4 different species names, can also provide additional support for the single-species contention. Assuming adequate sampling, and because no larvae have been observed with more than 5 rows of facets in the upper eye lobe, some change in eye morphology must occur, at least in those adults having eyes with 6 or more rows. Indeed, a series of steps must be involved in the acquisition of an eye with 19 facet rows. As is apparently true from existing larval descriptions, each individual does not pass through all increments of eye structure, i.e., always beginning with 2 rows of facets, progressing to 3, then to 4, etc., with increasing size. The single-species hypothesis need not address the latter because varying larval environments may induce different larval morphologies, as is evident in the development of other structures.

A number of subadult specimens encountered in the R/V *Gosnold* collections also support this hypothesis. These specimens each displayed oblong eyes (lower lobe width/upper lobe width  $\approx 1.0$ ) and a ratio of eye length to lower lobe width which would indicate *S. longicorne*. However, they possessed 6 facet rows in the upper eye in lateral view, and measurements of eye length, as well as the sixth abdominal segment, either definitely indicating *S. affine* or within the range of overlap of *S. affine* and *S. longicorne*. No sexually mature individuals were encountered having this intermediate

morphology, suggesting that the characters involved may be ontogenetic. The holotype of *S. longicorne* (7.3 mm female, BMNH 1940.7.10.1) is also of this intermediate form (Fig. 7), thus corresponding more closely to the current taxonomic conception of *S. affine*. Although the holotype was larger in size than the *Gosnold* subadults, determining the maturity of the specimen would have required dissection, and was not done.

*Ecology*.—The absence of one or more of the various forms from any one area further supports the hypothesis of environmentally influenced morphologies. For example, adults of the 2-faceted form (in lateral view = “*S. microphthalmma*”) were not found in the eastern Floridan collections perhaps because environmental conditions were unfavorable in that area for maintenance of such an animal. Likewise, larger forms (“*S. longicorne*”), capable of existing in colder, deeper waters, have been collected from higher (=cooler) latitudes than the shallow-living (=warmer water) forms. However, the existence of discontinuous distributions does not preclude the conspecific nature of these 4 forms. Rather, it indicates that each morphology is best suited to a limited set of environmental conditions, including ambient temperature, pressure, and light intensity level.

*Taxonomy*.—*Stylocheiron microphthalmma*, *S. suhmii*, *S. affine*, and *S. longicorne* are therefore best considered as interpopulational variants of a single polymorphic species, in which morphology is environmentally or ontogenetically influenced. The name *S. suhmii* has page priority and with strict adherence to Articles 23–24 of the International Code of Zoological Nomenclature (ICZN), the remaining 3 names become junior subjective synonyms. Article 15 of the ICZN furthermore prevents the use of *forma* designations.

As senior synonym, *Stylocheiron longicorne* might be preferable over the simultaneously published *S. suhmii*. As first revisor, I need not strictly adhere to page priority in designating the name best serving nomenclatural stability (see Recom. 24A of the ICZN). When factors including adequacy of description, condition of holotype, and familiarity of the species to the scientific community are considered, both names are of equal value. The only advantage in establishing priority of the name *S. longicorne* would be to allow continued use of the terminology “*S. longicorne* species group.” However, Hansen (1910) appears to have arbitrarily chosen *S. longicorne* to represent this group, without giving any explanation. Furthermore, the

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Fig. 7. *Stylocheiron longicorne*, holotype, 7.3 mm female, BMNH 1940.7.10.1: A, Entire specimen, left lateral view; B, Left eye, scale as in C; C, Right eye. In B and C, eyes are adjusted to direct lateral view with pins, to show 6 aligned rows of facets in each upper lobe; D, Sixth abdominal segment, left lateral view, retouched to show posterior margins of fifth and sixth segments. Scale = 1.0 mm (A), 0.25 mm (B–D).







species group category has no taxonomic status and seems primarily a grouping of convenience. Consequently, I designate *Stylocheiron suhmii* as senior synonym by page priority over *S. longicorne*. An emended description of *S. suhmii* reflecting this treatment is provided below. If a species group name is used at all, it should be termed the "*S. suhmii* species group" to avoid use of an invalid name.

Emended Description of  
*Stylocheiron suhmii* G. O. Sars, 1883

- Stylocheiron suhmii* G. O. Sars, 1883:31–32; 1885:142–144, pl. XXVII, figs. 1–4.—Hansen, 1905:30–31; 1910:119–120; 1912:277–278, pl. 11, fig. 3(a–b).—Lebour, 1926a:203–211, fig. 1(a–l), fig. 2(a–d); 1926b:773–774, fig. 4(p–s); 1926c:520–521, 524.—Ruud, 1936:16–17, 49–53, figs. 5, 17, Table 17.—Sheard, 1953:20, Tables 1, 2, 9.—Boden, 1954: 234, fig. 20(d–e).—Boden *et al.*, 1955:383–385, fig. 50(a–c).—Pillai, 1957:24.—Brinton, 1962a:175, figs. 87–88, Table 12; 1975:206, 256, figs. 109, 123b, Table 5.—Schroeder, 1971:116–122, fig. 30(a–c), Tables 2, 5–7, 10–12.—B. Casanova, 1972:180; 1974:111–118, figs. 28–30.—Costanzo and Guglielmo, 1976b:180, text-fig. 3, pl. 2, fig. 1.—Roger, 1976:104, Table 1.—Mauchline and Nemoto, 1977:287, fig. 4.—Lomakina, 1978:207–208, figs. 14(2), 125(1–2).
- S. suhmi*.—Ortmann, 1893:17–18.—Gurney, 1942:173, Table.—Brinton, 1967:475–477, 482, fig. 21.—Mauchline, 1967:34–36, fig. 18e.
- S. longicorne* G. O. Sars, 1883:32; 1885:144–145, pl. XXVII, fig. 5.—Hansen, 1908:92–93; 1910:120–121, pl. XVI, fig. 5(a–b); 1912:279–280, pl. 11, fig. 4(a–b).—Frost, 1935:447–451, pl. XIV(A–J), pl. XV(A–H), Table.—Ruud, 1936:15–16, 47–49, figs. 5, 17, 20, Table 16.—Banner, 1950:37–38, pl. IV, fig. 25a, Table 1.—Sheard, 1953:20, Tables 1–2, 9.—Boden, 1954:234–36, fig. 21(a–c).—Boden *et al.*, 1955:388–389, fig. 53(a–c).—Brinton, 1962a:190–193, figs. 93b, 98–100, Table 12; 1975:215–216, 258, figs. 115, 124(a–c), Table 5.—Mauchline, 1967:34–36, fig. 18g; 1971:13, pl. IV(14a–14g), Tables 1–4.—Schroeder, 1971:112–116, fig. 29(a–c), Tables 2, 5–7, 10–12.—B. Casanova, 1974:105–109, figs. 26–27.—Costanzo and Guglielmo, 1976b:180, text-fig. 4, pl. 2, fig. 2.—Roger, 1976:104, Table 1.—Mauchline and Nemoto, 1977:287, fig. 4.—Lomakina, 1978:211–212, figs. 7(12), 8(10), 11(3), 16, 128(1–4).
- S. mastigophorum* Chun, 1887:30–32, pl. IV, fig. 1–1a; 1896a:144–152, pl. IX, figs. 1–27, pl. X, figs. 1–19; 1896b:200–209, 215–228, text-fig. 4, pl. XVI, figs. 3, 7, pl. XIX, figs. 1–13.—Hansen, 1905:30–31.
- S. microphthalma* Hansen, 1910:117–118, pl. XVI, fig. 3(a–d).—Sheard, 1953:20, Tables 1–2.—Boden *et al.*, 1955:385–386, fig. 51(a–c).—Brinton, 1962a:172–175, figs. 85–86, Table 12; 1967:482; 1975:210–212, figs. 112(a–

b), 123g, Table 5.—Roger, 1976:104, Table 1.—Lomakina, 1978:208–209, figs. 4(4), 14(4), 126(1–4).

*S. microphthalmum*.—Zimmer and Gruner, 1956:253.

*S. affine* Hansen, 1910:118–120, pl. XVI, fig. 4(a–d); 1912:278–279.—Sheard, 1953:20, Tables 1, 2, 9.—Boden, 1954:232–234, fig. 20(a–c).—Boden *et al.*, 1955:382–383, fig. 49(a–c).—Pillai, 1957:22–24, fig. XI(1–3).—Brinton, 1962a:178–190, figs. 92–97, Table 12; 1967:475–477, fig. 19; 1975:208–210, 256, figs. 111, 123(d–f), 137, Table 5.—Mauchline, 1967:34–36, fig. 18C.—Schroeder, 1971:97–101, fig. 26(a–c), Tables 2, 5–7, 10–12.—Roger, 1976:104, Table 1.—Mauchline and Nemoto, 1977:287, fig. 4.—Silas and Mathew, 1977:578, fig. 5.—Lomakina, 1978:205–207, figs. 3(5), 124(1–3).

*S. affini*.—Wiebe, 1976:75, fig. 7 [lapsus].

*Description*.—Generic characters: Rostrum acute; sexually dimorphic, longer in female. Carapace lacking lateral denticles at ventral edge. Antennular peduncle without species-specific lobes or processes; segments sexually dimorphic, longer and thinner in female. Eyes bilobate. Mandible without palp. Maxillule without pseudoexopodite. Maxilla with reduced endopodite; endite of the protopodite not divided into 2 lobes. Third thoracic endopod greatly elongate, with strong terminal bristles. Seventh and eighth thoracic appendages reduced. Five photophores: one each on eyestalks, on bases of seventh thoracic appendages, and on ventral surface of first abdominal segment. Petasma with inner and medial lobes fused; secondary spinous process may be present; additional process absent. Thelycum formed solely by united plates from coxae of sixth thoracic appendages, with series of setae on anterior edge. Ova carried by female in ovisac.

Specific characters: Carapace weakly keeled in gastric region. Lower lobe of eye with numerous radiating ommatidia; upper lobe with 4 to over 200 enlarged parallel ommatidia, increasing in number with habitat depth or body size; ommatidia of lateral areas of eye rudimentary, transparent. Maxillae lacking suture line between lobe of third joint and endopod. Elongate third thoracic endopod terminating in “false chela” of 3 propodal spines opposing 5 dactylar spines; most medial propodal spine with 90° bend at tip. Abdominal segments unarmed.

Petasma with terminal and proximal processes blade-like distally, subequal in size; distal end of terminal process dentate in larger (? more mature) specimens; lateral process slightly smaller than preceding, distally rounded.

Thelycum with plates fused in anterior third of midventral line, widely diverging posteriorly; anterior edge bearing 2–5 primary, 2–4 secondary setae, increasing in number in larger (? more mature) specimens.

*Adult body length*.—5.5–15.3 mm.

*Distribution*.—Panoceanic from approximately 40°N to 40°S, and as far



as 63°N in the Atlantic (Dahl 1961). Epi- to mesopelagic, ranging primarily from 0–500 m in depth. In general, forms with larger eyes inhabit greater depths than those with smaller eyes. Does not undergo diel vertical migrations, but may be capable of daytime avoidance of collecting devices (Brinton 1967).

*Remarks.*—*Stylocheiron suhmii* was originally described from a single female specimen having eyes “much narrowed in the upper part” (G. O. Sars 1883:31), but without reference to the exact number of ommatidia. Hansen (1910:119–120) re-examined Sars’ holotype, stating that it displayed “three well developed crystal cones in a transverse row,” thus apparently (and as will be seen, erroneously) emending the description of *S. suhmii*. In the same work, Hansen also named 2 new species, distinguished from *S. suhmii* by number of ommatidia visible in lateral view: *S. microphthalma* with 2, and *S. affine* with 4–6.

My re-examination of the holotype of *S. suhmii* (6.1 mm\* female, BMNH 1981.87) revealed a lateral count of 2 rows in the upper eye lobe (Fig. 8C–F), rather than 3 as described by Hansen (1910). The specimen (Fig. 8A), permanently mounted on a microslide, has a slightly damaged right eye (Fig. 8E–F), resulting in distortion which brought the “incorrect” anterolateral viewing angle (previously discussed) into view, and apparently caused Hansen’s erroneous emendation. Moreover, proportions of the sixth abdominal segment ( $L/D = 1.5$ ; Fig. 8B) and the eye structure of the holotype of *S. suhmii* agree with the currently accepted characteristics (Table 2) and with the syntypes (see Appendix) of *S. microphthalma*. It is thus apparent that Hansen’s misinterpretation of the eye of Sars’ holotype was the primary error leading him to establish *S. microphthalma*. The latter species, supposedly distinguished from *S. suhmii* by having only 2 rows of facets, is identical to the holotype, and becomes a junior subjective synonym, of *S. suhmii*, regardless of any other conclusion reached by this study.

Although never carried to such an extent, the synonymizing of *S. longicorne* with *S. suhmii* is not entirely new. Both species were described by G. O. Sars (1883) and have been synonymized several times. Hansen (1905) considered them to be immature (*S. suhmii*) and adult (*S. longicorne*) individuals of the same species, and designated *S. suhmii* as the valid name. Ortmann (1905) also followed this practice. In addition, Hansen (1905) synonymized *S. mastigophorum* Chun, 1887, with *S. suhmii*, based on identical structures of the first 2 pairs of thoracic legs. This was done on the advice of Calman (in Hansen 1905), who, in comparing the holotype of *S. longi-*

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\* The value of 8 mm usually cited as the maximum size of *S. suhmii* is attributable to this specimen, as originally cited by Sars (1883). Personal examination revealed that this length included the antennae and that the body length is actually 6.1 mm.



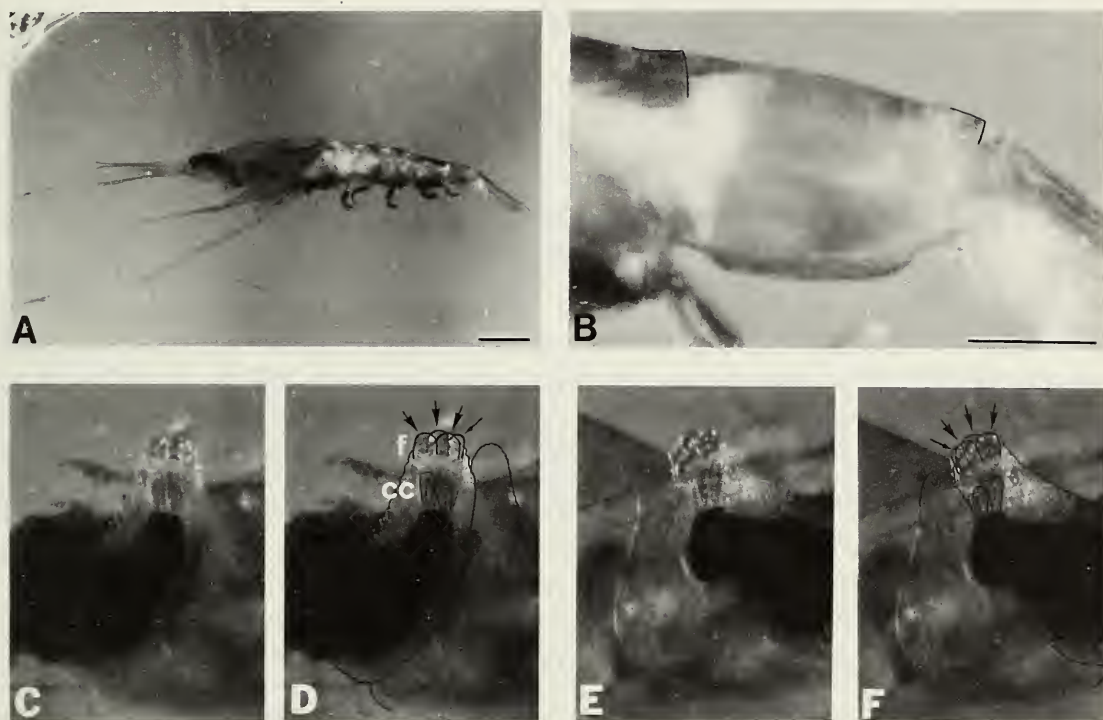


Fig. 8. *Stylocheiron suhmii*, holotype, 6.1 mm female, BMNH 1981.87: A. Entire specimen, left lateral view; B. Sixth abdominal segment, left lateral view, retouched to show posterior margins of fifth and sixth segments; C. Left eye; D. Same, retouched to emphasize enlarged ommatidia; E. Right eye; F. Same, retouched as in D. Lower portion of right eye is slightly damaged. Arrows indicate the enlarged facets; smaller arrow points to fourth and smallest facet in each upper lobe. cc, crystalline cones; f, corneal facets. Magnification in C–F as in B. Scale = 1.0 mm (A), 0.25 mm (B–F).

*corne* with the description and figures of *S. mastigophorum*, found Chun's distinctions between the 2 species in the thoracic legs to be without value. Hansen (1908) later resurrected *S. longicorne*, and cancelled his "first revisor" status, when additional material prompted the descriptions of *S. microphthalmma* and *S. affine*, published in 1910. *S. mastigophorum* then became synonymous in part (Hansen 1910) with both *S. suhmii* and *S. longicorne*, according to Chun's (1896b) illustrations of their respective eye structures. Finally, in a catalog from the National Museum of Ireland, the 2 names appeared again in synonymy: "*Stylocheiron longicorne* G. O. Sars = *Stylocheiron suhmi* [sic] G. O. Sars" (O'Riordan [1969]:52), although with the name *S. longicorne* having apparent priority.

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#### Literature Cited

- Baker, A. D. C. 1970. The vertical distribution of euphausiids near Fuerteventura, Canary Islands ('Discovery' Soud Cruise, 1965).—*Journal of the Marine Biological Association of the United Kingdom* 50(2):301–342.
- Banner, A. H. 1950. A taxonomic study of the Mysidacea and Euphausiacea (Crustacea) of the northeastern Pacific. Part III. Euphausiacea.—*Transactions of the Royal Canadian Institute* 28(58):1–62, pls. 1–4.
- Boden, B. P. 1954. The euphausiid crustaceans of southern African waters.—*Transactions of the Royal Society of South Africa* 34(1):181–243.
- , M. W. Johnson, and E. Brinton. 1955. The Euphausiacea (Crustacea) of the North Pacific.—*Bulletin of the Scripps Institution of Oceanography* 6:287–400.
- Brinton, E. 1962a. The distribution of Pacific euphausiids.—*Bulletin of the Scripps Institution of Oceanography* 8(2):51–270.
- . 1962b. Two new species of Euphausiacea, *Euphausia nana* and *Stylocheiron robustum* from the Pacific.—*Crustaceana* 4(3):167–179.
- . 1967. Vertical migration and avoidance capability of euphausiids in the California Current.—*Limnology and Oceanography* 12(3):451–483.
- . 1975. Euphausiids of southeast Asian waters.—*Naga Report* 4(5):1–287.
- Casanova, B. 1972. Clé de détermination des larves calyptopis des Euphausiacés de Méditerranée.—*Crustaceana* 22(2):178–180.
- . 1974. Les Euphausiacés de Méditerranée. (Systématique et développement larvaire. Biogéographie et biologie)—Ph.D. Dissertation, l'Université de Provence (Aix-Marseille I), 380 pp. [As cited by Brinton, 1975.]
- Casanova, J. P. 1977. La faune pélagique profonde (zooplancton et micronecton) de la province Atlanto-Méditerranéenne: aspects taxonomique, biologique et zoogéographique.—Ph.D. Dissertation, l'Université de Provence (Aix-Marseille I), 455 pp.
- Chun, C. 1887. Die pelagische Thierwelt in grösseren Meerstiefen und ihre Beziehungen zu der Oberflächenfauna.—*Bibliotheca Zoologica*, Stuttgart 1:1–66, 5 pls.



- . 1896a. Atlantis. Biologische Studien über pelagische Organismen. V. Über pelagische Tiefsee Schizopoden.—*Bibliotheca Zoologica*, Stuttgart 7(19, 3):137–190, pls. VIII–XV.
- . 1896b. Atlantis. Biologische Studien über pelagische Organismen. VI. Leuchtorgane und Facettenaugen.—*Bibliotheca Zoologica*, Stuttgart 7(19, 4):191–262, pls. XVI–XX.
- Costanzo, G., and L. Guglielmo. 1976a. Diagnostic value of the thelycum in euphausiids. I. Mediterranean species (first note).—*Crustaceana* 31(1):45–53, pls. 1–4.
- , and ———. 1976b. Diagnostic value of the thelycum in euphausiids. I. Mediterranean species (second note).—*Crustaceana* 31(2):178–180, pls. 1–3.
- Dahl, E. 1961. A record of the euphausiacean *Stylocheiron longicorne* from west Norway.—*Sarsia* 4:39–42.
- Einarsson, H. 1942. Notes on Euphausiacea I–III. On the systematic value of the spermatheca, on sexual dimorphism in *Nematoscelis* and on the male in *Bentheuphausia*.—*Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 106:263–286.
- Frost, W. E. 1935. Larval stages of the euphausiids *Nematoscelis megalops* (G. O. Sars) and *Stylocheiron longicorne* (G. O. Sars) taken off the south-west coast of Ireland.—*Proceedings of the Royal Irish Academy XLII* (B, 16):443–458, pls. XII–XV.
- Gurney, R. 1942. Larvae of Decapod Crustacea.—The Ray Society, London, 306 pp.
- Hansen, H. J. 1905. Preliminary report on the Schizopoda collected by H. S. H. Prince Albert of Monaco during the cruise of the *Princesse-Alice* in the year 1904.—*Bulletin du Musée Océanographique de Monaco* No. 30:1–32.
- . 1908. Crustacea Malacostraca. I.—*Danish Ingolf-Expedition* 3(2):1–120.
- . 1910. The Schizopoda of the Siboga Expedition.—*Siboga-Expeditie Monograph* 37:1–123, 16 pls.
- . 1912. Reports on the scientific results of the expedition to the tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer 'Albatross', from August, 1899, to March, 1900, Commander Jefferson F. Moser, U. S. N., commanding. XVI. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer 'Albatross', from October, 1904, to March, 1905, Lieut. Commander L. M. Garrett, U. S. N., commanding. XXVII. The Schizopoda.—*Memoirs of the Museum of Comparative Zoology at Harvard College* 35(4):175–296, 12 pls.
- Kampa, E. M. 1965. The euphausiid eye—a re-evaluation.—*Vision Research* 5:475–481.
- Lebour, M. V. 1926a. The young of *Stylocheiron suhmii* G. O. Sars and *Stylocheiron abbreviatum* G. O. Sars (Crustacea), from Mediterranean plankton collected by Mr. F. S. Russell in the neighbourhood of Alexandria, Egypt.—*Proceedings of the Zoological Society of London* 1926(1):203–211.
- . 1926b. On some larval euphausiids from the Mediterranean in the neighbourhood of Alexandria, Egypt, collected by Mr. F. S. Russell.—*Proceedings of the Zoological Society of London* 26(3):765–776.
- . 1926c. A general survey of larval euphausiids, with a scheme for their identification.—*Journal of the Marine Biological Association of the United Kingdom* 14(2):519–527.
- Lomakina, N. B. 1978. Euphausiids (Euphausiacea) of the World Ocean.—'Nauka,' Leningrad, 222 pp. [Translated from Russian by C. L. Van Dover, 1980–1981.]
- Mauchline, J. 1959. The development of the Euphausiacea (Crustacea) especially that of *Meganyctiphanes norvegica* (M. Sars).—*Proceedings of the Zoological Society of London* 132(4):627–639.
- . 1967. The feeding appendages of Euphausiacea (Crustacea).—*Journal of Zoology*, London 153(1):1–43.
- . 1971. Euphausiacea. Larvae.—*Conseil International pour l'Exploration de la Mer*, Zooplankton Sheet 135/137, 16 pp.

- , and L. R. Fisher. 1969. The biology of euphausiids.—*Advances in Marine Biology* 7:i-ix + 1-454.
- , and T. Nemoto. 1977. Integumental sensilla of diagnostic value in euphausiids.—*Journal of the Oceanographical Society of Japan* 33(5):283-289.
- Mayr, E. 1969. *Principles of Systematic Zoology*.—McGraw-Hill, New York, 428 pp.
- O'Riordan, C. E. 1969. A catalog of the collection of Irish marine Crustacea in the National Museum of Ireland.—Government Publications Office, Dublin, 98 pp.
- Ortmann, A. E. 1893. Decapoden und Schizopoden.—*Ergebnisse der Plankton - Expedition der Humboldt-Stiftung* 2,G.b.:1-120, 7 pls., 3 maps.
- . 1905. Schizopods of the Hawaiian Islands collected by the steamer Albatross in 1902.—*Bulletin of the U.S. Fish Commission* 1903(3):961-973.
- Pillai, N. K. 1957. Pelagic Crustacea of Travancore, II. Schizopoda.—*Bulletin of the Central Research Institute, University of Travancore, Ser. C. Natural Sciences* 57(1):1-28.
- Ponomareva, L. A. 1963. Euphausiids of the North Pacific, their distribution and ecology.—*Izdatel'stvo Akademii Nauk S.S.S.R., Moskva*, 154 pp. [Translated from Russian by Israel Program for Scientific Translations, Jerusalem, 1966.]
- Roger, C. 1974. Répartitions bathymétriques et migrations verticales des Euphausiacés (Crustacés) dans les zones de pêche au thon du Pacific sud-tropical.—*Cahiers ORSTOM, Océanographie* 12(4):221-239.
- . 1976. Fecundity of tropical euphausiids from the central and western Pacific Ocean.—*Crustaceana* 31(1):103-105.
- Ruud, J. T. 1936. D. 6. Euphausiacea.—*Report on the Danish Oceanographical Expeditions 1908-1910 to the Mediterranean and Adjacent Seas. Vol. II. Biology.* 86 pp.
- Sars, G. O. 1883. Preliminary notices on the Schizopoda of H. M. S. 'Challenger' Expedition.—*Forhandlingar Videnskabs-Selskabets i Kristiania* No. 7:1-43.
- . 1885. Report on the Schizopoda collected by H. M. S. 'Challenger' during the years 1873-1876.—*Challenger Reports, Zoology* 13(37):1-228, pls. 1-38.
- Schroeder, W. W. 1971. The distribution of euphausiids in the oceanic Gulf of Mexico, the Yucatan Strait, and the northwest Caribbean.—Ph.D. Dissertation, Texas A & M Univ., 174 pp.
- Sheard, K. 1953. Taxonomy, distribution and development of the Euphausiacea (Crustacea).—*Reports of the B.A.N.Z. Antarctic Research Expedition 1929-1931, Series B (Zoology and Botany)* 8(1):1-72.
- Silas, E. G., and K. J. Mathew. 1967. *Stylocheiron indicus*, a new euphausiid (Crustacea: Euphausiacea) from Indian seas.—*Current Science* 36(7):169-172.
- , and ———. 1977. A critique to the study of larval development in Euphausiacea.—*Proceedings of Symposium on Warm Water Zooplankton, Spec. Publ. UNESCO/NIO*, pp. 571-582.
- Wiebe, P. H. 1976. The biology of cold-core rings.—*Oceanus* 19(3):69-76.
- Zimmer, C., and H.-E. Gruner. 1956. Dr. H. G. Bronns Klassen und Ordnungen des Tierreichs. Fünfter Band: Arthropoda. I. Abteilung: Crustacea. 6. Buch, III. Teil, Euphausiacea. 1. Lieferung.—*Akademische Verlagsgesellschaft, Leipzig*, 2 parts, 286 pp.

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## Appendix

Material examined, *Stylocheiron longicorne* species group.

### I. *Stylocheiron suhmii* G. O. Sars, 1883.

A. Specimens with 2 rows of facets visible in lateral view, formerly



referable to *S. microphthalma*: INDO-PACIFIC: North of New Guinea: 1 ♀ (holotype of *S. suhmii*), BMNH 1981.87.—Indonesia: 3 ♀♀ (syntypes of *S. microphthalma*), *Siboga* Sta. 104–108, ZMA Sch. 150.143; 3 ♂♂, 12 ♀♀ (illustrated syntypes (Hansen 1910) of *S. microphthalma*), *Siboga* Sta. 128, ZMUC; 2 ♀♀ (syntypes of *S. microphthalma*), *Siboga* Sta. 129, ZMA Sch. 150.144; 1 ♀ with empty ovisac (syntype of *S. microphthalma*), *Siboga* Sta. 184, ZMA Sch. 150.145; 2 ♀♀ (syntypes of *S. microphthalma*), *Siboga* Sta. 276, ZMA Sch. 150.146; 1 ♂, 1 ♀, *Albatross* Sta. 5616, ZMUC.—Fiji Islands: 1 ♀, ZMUC.—China Sea: 2 ♂♂, 1 ♀, *Albatross* Sta. 5320, USNM 49355.—ATLANTIC: Tropical Atlantic: 2 subadults, BMNH 1886.37 (in part).—Bermuda: 2 ♂♂, 10 ♀♀, 29 subadults, BMNH 1965.8.23.346–358 (in part).

B. Specimens with 3 rows of facets visible in lateral view, formerly referable to *S. suhmii* (sensu Hansen): INDO-PACIFIC: Philippine Islands: 1 ♂, 1 subadult, BMNH 1886.37 (in part).—China Sea: 1 specimen, BMNH 1886.37 (in part).—Fiji Islands: 1 ♂, 2 ♀♀, ZMUC.—ATLANTIC: Western Atlantic: 10 ♂♂, 41 ♀♀, *Bache* Sta., USNM 62294 (in part); 1 ♀, *Bache* Sta., USNM 62295 (in part).—Tropical Atlantic: 1 ♂, BMNH 1886.37 (in part).—eastern Florida: 6 ♂♂, 7 ♀♀, *Gosnold* Sta. 130; 1 ♂, *Gosnold* Sta. 131; 13 ♂♂, 21 ♀♀, 1 other specimen, *Gosnold* Sta. 144; 14 ♂♂, 24 ♀♀, *Gosnold* Sta. 159; 54 ♂♂, 55 ♀♀ (3 ovigerous), *Gosnold* Sta. 160; 2 ♂♂, 3 ♀♀, *Gosnold* Sta. 172; 7 ♂♂, 7 ♀♀, *Gosnold* Sta. 173.—Bermuda: 2 ♂♂, 14 ♀♀, 5 subadults, BMNH 1965.8.23.346–358 (in part).

C. Specimens with 4–8 rows of facets visible in lateral view, formerly referable to *S. affine*: INDO-PACIFIC: Indonesia: 6 ♀♀, 19 other specimens (syntypes of *S. affine*), *Siboga* Sta. 66, ZMUC; 1 ♀ (syntype of *S. affine*), *Siboga* Sta. 118, ZMA Sch. 150.150; 3 ♀♀ (syntypes of *S. affine*), *Siboga* Sta. 129, ZMA Sch. 150.151; 1 ♀, 7 other specimens (syntypes of *S. affine*), *Siboga* Sta. 141, ZMA Sch. 150.152; 4 ♀♀ (one ovigerous) (syntypes of *S. affine*), *Siboga* Sta. 143, ZMA Sch. 150.153; 5 ♀♀ (syntypes of *S. affine*), *Siboga* Sta. 148, ZMA Sch. 150.154; 1 ♀ (syntype of *S. affine*), *Siboga* Sta. 157, ZMA Sch. 150.147; 2 ♂♂, 6 ♀♀, 4 other specimens (syntypes of *S. affine*), *Siboga* Sta. 185, ZMA Sch. 150.148; 6 ♂♂, 20 ♀♀, 9 other specimens (illustrated syntypes (Hansen 1910) of *S. affine*), *Siboga* Sta. 203, ZMUC; 1 ♀, 29 subadults (syntypes of *S. affine*), *Siboga* Sta. 220, ZMUC; 5 ♂♂, 11 ♀♀, 3 other specimens (syntypes of *S. affine*), *Siboga* Sta. 276, ZMA Sch. 150.149.—Philippine Islands: 3 ♂♂, 7 ♀♀, *Albatross* Sta. 5456, ZMUC; 7 ♂♂, 37 ♀♀, 10 other specimens, *Albatross* Sta. 5456, USNM 49378.—Tropical eastern PACIFIC: 1 ♀, ZMUC; 3 ♀♀, *Albatross* Sta. 4634, ZMUC.—AT-

LANTIC: Western Atlantic: 24 ♂♂, 50 ♀♀, Bache Sta., USNM 62295 (in part).—Bermuda: 1 ♀, BMNH 1965.8.23.346–358 (in part).—eastern Florida: 19 ♂♂, 17 ♀♀, *Gosnold* Sta. 144; 5 ♂♂, 6 ♀♀, *Gosnold* Sta. 159; 2 ♂♂, 14 ♀♀, *Gosnold* Sta. 160; 1 ♂, 2 ♀♀, *Gosnold* Sta. 172; 2 ♂♂, 6 ♀♀, *Gosnold* Sta. 173.

D. Subadult specimens with 6 rows of facets visible in lateral view, intermediate in morphology to *S. affine* and *S. longicorne* (sensu Brinton): ATLANTIC: south of Cape of Good Hope: 1 ♀ (holotype of *S. longicorne*), BMNH 1940.7.10.1.—eastern Florida: 2 ♂♂, 2 ♀♀, *Gosnold* Sta. 144; 1 ♂, 1 ♀, *Gosnold* Sta. 159; 1 ♀, *Gosnold* Sta. 160; 2 ♀♀, *Gosnold* Sta. 172.

E. Specimens with 7–19 rows of facets visible in lateral view, formerly referable to *S. longicorne*: ATLANTIC: Western Atlantic: 21 ♂♂, 65 ♀♀, 9 other specimens, *Bache* Sta., USNM 62295 (in part); 1 ♀, *Bache* Sta., USNM 92294 (in part).—Gulf of Mexico: 2 ♂♂, 4 ♀♀, *Alaminos* Sta. 66.A.5.3, USNM 135313.—eastern Florida: 23 ♂♂, 41 ♀♀, *Gosnold* Sta. 144; 2 ♂♂, 4 ♀♀, *Gosnold* Sta. 159; 1 ♀, *Gosnold* Sta. 160; 5 ♀♀, *Gosnold* Sta. 172.

F. Other specimens previously misidentified as one of the forms of this species: *S. affine*: 1 specimen, off western Africa, *Atlantide* Sta. 91, ZMUC [not genus *Stylocheiron*, according to photophore arrangement]; 1 specimen, off western Africa, *Atlantide* Sta. 52, ZMUC [mysid, according to statocyst in uropod].—*S. suhmii*: 1 specimen, tropical Atlantic, BMNH 1886.37 (in part) [= *S. carinatum*].

## II. Other members of the *Stylocheiron longicorne* species group:

A. *Stylocheiron elongatum* G. O. Sars, 1883: ATLANTIC: Western Atlantic: 18 ♂♂, 21 ♀♀ (7 ovigerous), 6 subadults, *Bache* Sta., USNM 62293.—eastern Florida: 10 ♂♂, 31 ♀♀ (4 ovigerous), *Gosnold* Sta. 144; 3 ♂♂, *Gosnold* Sta. 159; 1 ♀, *Gosnold* Sta. 160; 4 ♂♂, 15 ♀♀ (2 ovigerous), 5 other specimens, *Gosnold* Sta. 172.